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THE INTEGUMENTARY SENSE ORGANS OF THE LARVÆ OF RHIPICEPHALINÆ (ACARINA)[1]

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In 1938 Delpy published a short paper describing the location and morphology of the so-called spiracles or respiratory plates ("stigmates respiratoires") of various Ixodid larvæ. He examined for the purpose *Hyalomma dromedarii* Koch, *H. impressum* Koch, *Boophilus annulatus* Say, *Rhipicephalus bursa* Can. and Fanz., and *Hæmaphysalis cinnabarina punctata* Can. and Fanz. Delpy's description is brief and lacks illustrations. He thought that he saw within each "spiracle" 1 or 2 pores, sometimes reduced in size, leading into an atrium provided with two valves at the entrance. The base of the atrium he described as pierced with an opening, and Delpy considered it possible that a tracheal tube was attached at this point.

With regard to their position, Delpy distinguished coxal and abdominal spiracles. The coxal spiracles are in three pairs, placed behind each of the six coxæ. The abdominal spiracles vary greatly in number and position according to the genus. *Hæmaphysalis* is said to have four pairs, *Hyalomma* and *Rhipicephalus* only one pair, while they are entirely lacking in *Boophilus*.

Delpy was not the first, however, to describe supposed spiracles in Ixodid larvæ. Salmon and Stiles (1902) saw

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them before, and they were also mentioned by Oudemans (1906), Zebrowski (1926) and Cooley (1938).

All these authors were mistaken in the interpretation of the function of the organ they had seen. The larvæ of the Ixodidæ do not possess any special respiratory organs. Only Samson (1908) correctly recognized that the so-called "larval spiracles" described by Salmon and Stiles were actually the terminal pores of integumentary sense organs. This correction was, however, overlooked up to quite recently. Even Vitzthum, in his account of the Acarina for "Bronn's Klassen und Ordnungen des Tierreichs" (1940), adopted in detail the description and views of Delpy.

K. W. Neumann (1942) and Elishewitz (1942) first re-examined these structures in an attempt to decide whether they were respiratory organs or integumentary glands. Serial sections of larvæ of *Dermacentor, Hæmaphysalis, Hyalomma* and *Ixodes* convinced Neumann that neither the Ixodinæ (Prostriata) nor the Rhipicephalinæ (Metastriata) have respiratory organs and that the structures thus far interpreted as spiracles are really integumentary glandular organs.

According to Neumann, these organs are in a direct view more or less oval in outline. "A broad ellipsoid chitinized frame at the periphery is attached to the surrounding cuticula by means of a narrow, prominent, striated edge. The lumen also is oval and contains two parallel, non-contiguous lips. Two small protuberances of the frame extend on each side into the lumen, keeping the lips from touching each other. By lowering the objective, a small circular opening may be recognized in the center between the lips."

"In a side view of the entire organ or in a section, the structure is also more or less elongate oval. The walls consist of a rather thick layer of chitin, decreasing in thickness from the base toward the surface opening. A short duct leads from the base toward the interior of the body. On either side of the mouth of this duct a tooth, anchored to the base of the organ, extends up into its lumen. Serial sections show that these teeth arise from a folding of the walls. Their length is approximately three-fourths of that of the entire organ."

"To what do these several parts correspond? The broad frame is the wall, the lips are the teeth, and the circular opening is the mouth of the short duct." (See Pl. 1, fig. 1.)

"The organ is securely anchored in the cuticula by the upper third of its length. The subjacent hypodermal cells are broader than high and surround the organ. The adjacent cells (?generative cells) are much higher than broad. Only two seem to be present, placed parallel to the margins of the lips. A large cell, considerably broader than high, lies beneath the organ, in close contact with the entire basal surface. The duct mentioned before is never long enough to pierce this basal cell, but ends with it without tapering downward. The duct is never lined with a tænidium. So far as can be detected, the plasma of this cell is slightly granular, but a prominent clear spot in the center may be interpreted as an internal vesicle. It follows from this description that the structure is an integumentary glandular organ, not a larval respiratory organ with a spiracle and a rudimentary trachea."

So much for K. W. Neumann's account of the morphology of his integumentary sense organ. In addition he discusses the number and position of these organs in various genera and believes to be justified in stating that originally two pairs were present. According to his account, all the spiracle-like organs show essentially the same structure, though they are sometimes reduced in size, and they seem undoubtedly to be peculiar to the larvæ. He does not mention any other integumentary sense organs besides these so-called "spiracles."

P. Schulze (1942*a*) published a detailed study of the integumentary sense organs of adult ticks and found, besides true sensory setæ (sensilla trichoidea), four other types of sensilla which he called *Sensilla auriformia* (ear-shaped organs), *Sensilla sagittiformia* (arrow-shaped organs), *Sensilla hastiformia* (spear-shaped organs), and *Sensilla laterniformia* (lantern-shaped organs).

Large numbers of these organs are located within the hard and soft chitinized integument of the body. On the other hand they are sparse on the legs and palps and,

strangely enough, seem to be entirely missing on the chelicerae. Characteristic for these sensilla is their connection with two glandular cells which extend partially into the sensory duct. These cells secrete into the duct a substance which emerges at the surface after passing an end organ. P. Schulze assumes that the secretion serves as a protective coating against evaporation within the sensillum and on the outer surface, and also as a chemical means of recognition between opposite sexes and individuals of one species.

The sensory function of the sensilla auriformia seems to be of a proprio-receptive nature, serving to perceive changes or shifts within the chitin. It is probable that the other three types, grouped together as "tuft-shaped" sense organs or krobylophores, are vibro-chemoreceptive organs, which react at the same time to chemical as well as to seismic stimulation. They evidently play an important part in the sexual life of the ticks.

We examined the larvæ of *Rhipicephalus sanguineus* Latr., *Rh. appendiculatus* Neum., *Rh. bursa* Can. and Fanz., *Rh. evertsi* Neum., *Rh. simus* Koch, *Hyalomma dromedarii* Koch, and *Boophilus calcaratus* Birula.

The larvæ were merely mounted whole on microscopic slides in Berlese's medium, a procedure which we found to be superior for our purpose to all other methods of mounting. Owing to prevailing conditions we were unable to make sections.

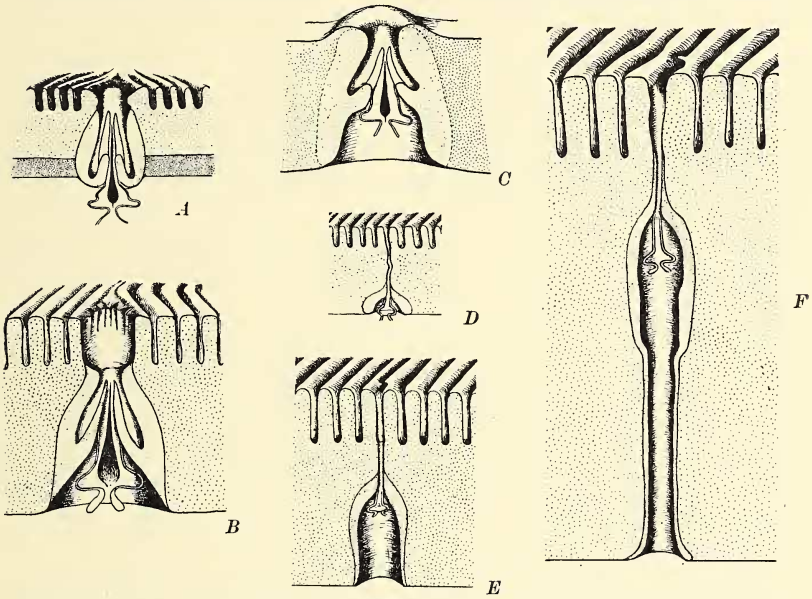
We were able to ascertain that the larvæ are not equipped with peculiar integumentary sense organs. On the contrary we found much the same organs present as in the adults and nymphs. In the larvæ, however, sensilla laterniformia seem to be lacking and the other types of sensilla are to some extent more primitive in development. The organs are distributed over the entire body in fixed numbers and in a definite arrangement.

A detailed account of the three types of sensilla mentioned above follows.

1. Sensilla sagittiformia (arrow-shaped organs)

The sensillum sagittiforme represents a new mode of sensory organ, called by P. Schulze a krobylophore sen-

sory organ, because a tuft-shaped structure is its most striking characteristic. In the adult tick he described this organ as follows in side view (Pl. 1, fig. 2): "The distal portion of the chitinized passage or lumen appears arrow-shaped. Below this lies a narrow pagoda-shaped 'tuft' chamber and farther inside a small, more or less spheroidal 'terminal chamber.' This is separated from



Text-figure 1. A, Sensillum sagittiforme of the opisthosoma of *Rhipicephalus appendiculatus* Neum. B, Same in the larva. C, Same in the nymph. D, Sensillum hastiforme of *Rhipicephalus appendiculatus* Neum. E, Same in the nymph. F, Same in the adult female.

the middle chamber by projecting ledges which leave room only for a small circular opening. The innermost chamber is attached to a simple duct into which the glandular cells extend, enveloping the nerve cells. The surrounding chitin is especially thick beneath the lower portion of the 'arrow points.' The nerve cells decrease in size as they enter the 'terminal chamber.' The axial fiber is attached to a strong scolopale which enlarges to

form a knot and then tapers down, becoming pointed again upon entering the 'pagoda-shaped chamber' in which the 'tuft' is located. This tuft has much the shape of a gas flame and is not chitinized but of a uniform structure, although at times it seems to be somewhat fibrillar."

The larvæ we examined all show, contrary to Delpy's description, four pairs of spiracle-like structures, three of them behind the coxæ, the fourth on the opisthosoma (Pl. 2, figs. 4 and 5). A comparison of their inner structure (Text-fig. 1A–C) with P. Schulze's description and drawings clearly shows that these so-called "larval spiracles" are in reality sensilla sagittiformia. The finer structure of the organ is best seen in the opisthosomal pair of the larvæ of *Rhipicephalus appendiculatus* and *Boophilus calcaratus*. It is pear-shaped and pierces with its conical end the integument on the dorsal face of the fourth festoon. The walls are of thick chitin, the chitinous capsule being 0.012 to 0.016 mm. long and 0.011 to 0.014 mm. broad. A funnel-shaped fold is visible within the capsule. The narrow ends of this capsule, pointing toward the opening, are less strongly chitinized and look in direct view like a pair of lips lying within the capsule (compare Pl. 1, fig. 1). Within these lips lies the tuft-like structure, surrounded by a fine pagoda-like contour.

The sensilla sagittiformia behind the second and third coxæ are very similar in structure to the opisthosomal pair described above. On the other hand, the pair located behind the first coxæ at the edge of the scutum seems to have a strikingly thick-walled capsule which is fully embedded in the chitin of the scutum. It is 0.019 to 0.022 mm. long, 0.016 to 0.022 mm. wide at the base, with the opening 0.011 to 0.014 mm. in diameter. The "tuft" is difficult to recognize here, but is shaped as in the other pairs.

2. Sensilla hastiformia (spear-shaped organs)

The sensilla hastiformia, as described by P. Schulze for the adult ticks, are much smaller than the arrow-

shaped organs. He was unable to make out all the details of the terminal apparatus, but he presumed that they correspond in general to those of the sensilla sagittiformia and that a tuft-shaped structure is also present. The main difference lies, according to Schulze, in the upper portion of the passage leading to the outside. This lacks the long receding arrow-points, so that the "pagoda-shaped chamber," formed by these points, is also missing. The passage is distinctly spear-shaped, in as much as it expands into two mainly horizontal projections at the base.

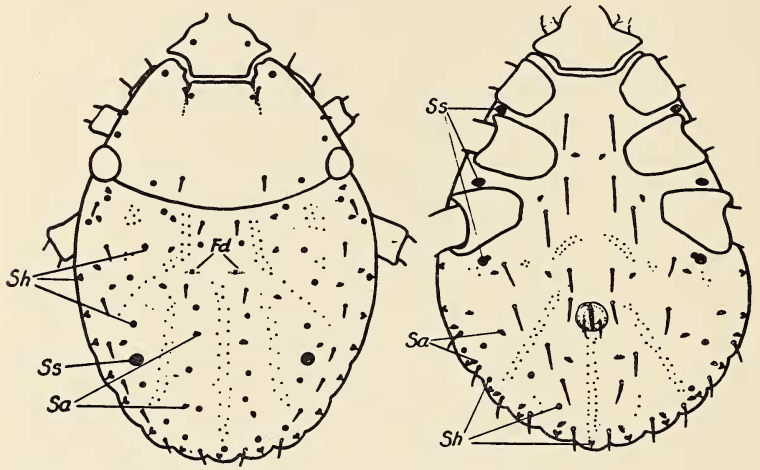
The larval sensillum hastiforme could only be recognized as such after comparing it with the corresponding organ in nymphs and adults (Text-fig. 1, D–F). It lies as a short funnel-shaped structure in the lower part of the integument, which it pierces by means of a narrow passage, ending between the outer folds. The funnel-shaped portion is approximately 0.008 mm. in diameter and 0.005 mm. deep. The walls are about 0.002 mm. thick and the passage is roughly 0.008 mm. long.

We were also unable to recognize the finer structure of the organ, nor could we find anything comparable to a "tuft." In direct view the organ has the appearance of a ring, 0.008 mm. in diameter. Further details cannot be recognized, but by lowering the objective the duct leading inside the body may be followed.

The larvæ of *Rhipicephalus appendiculatus* Neum., *Rh. sanguineus* Latr., *Rh. bursa* Can. and Fanz., and *Rh. evertsi* Neum. studied by us, all have 54 sensilla hastiformia on the body proper; we did not examine the legs. The sensilla are placed strictly symmetrically and neither their position nor their number seem to vary to any extent (Pl. 3, fig. 6). One pair is located on the capitulum, occupying the position taken by the areæ porosæ of the adult female tick. Five pairs are situated on the scutum and nine pairs on the alloscutum, four of these dorsal, one subdorsal and four sublateral. In addition eight pairs are found on the edge of the alloscutum, one sensillum being placed on the edge of each festoon (or parmula), except on the middle festoon. The ar-

rangement of these eight pairs is therefore metameric and seems to be derived from the primitive segmentation of the opisthosoma.

The "foveæ dorsales" of the larva consist of only one sensillum hastiforme each. The integumental folds bend around their openings, whereas on the contrary the openings of the other sensilla hastiformia lose themselves among the folds of the integument. Aside from the fact



Text-figure 2. Arrangement of the integumentary sense organs of the larva of *Hyalomma dromedarii* Koch: Fd, foveæ dorsales; Sa, sensilla auriformia; Sh, sensilla hastiformia; Ss, sensilla sagittiformia.

that the openings are more conspicuous, they do not differ from the usual type of sensilla hastiformia.

Ventrally the body bears four pairs of sensilla hastiformia. One pair lies very close to the sensillum sagittiforme of the third coxa. In *Rh. appendiculatus* it is enclosed by the capsule of the sensillum sagittiforme, so that it is difficult to see. Though closely adjacent to it in the other species, the sensillum hastiforme is nevertheless clearly set off.

The number and the arrangement of the sensilla hastiformia of the larva of *Boophilus calcaratus* Birula (Pl. 3, fig. 7) are similar to those of the *Rhipicephalus,* ex-

cept that we were unable to discover the two foremost pairs on the ventral side and that they seem to be missing also on the fourth and fifth festoons counting from the middle.

The larva of *Hyalomma dromedarii* Koch (Text-fig. 2) possesses more sensilla hastiformia than that of *Rhipicephalus*. It should be mentioned especially that the middle festoon also bears a terminal and a dorsal unpaired sensillum. In addition a sensillum hastiforme is located on the dorsal side adjacent to each of the second, third and fourth festoons. It is noteworthy that two pairs of sensilla hastiformia, instead of one pair, were found on the capitulum of one specimen in the position of the areæ porosæ of the adult female.

3. Sensilla auriformia (ear-shaped organs)

The sensilla auriformia discovered by P. Schulze (1942*a*) in adult ticks may be traced back with certainty to setæ or hairs. They are located directly under the cuticula and consist each of a flat disk, usually inclined a little toward one side, so that it closes outwardly the sensory duct ascending from below, like a lid with overlapping edges (Pl. 1, fig. 3). The disks vary in details and have the shape of an ear, a megaphone or a bell. Their openings face various directions, so that it is possible to see one sensillum in direct view and the other in side view when examining two of them placed close together.

The larval ticks also possess these sensilla in typical form, but the organs are smaller than in the adult. The disk is approximately 0.009 mm. in diameter. Arrangement and number again seem to be strictly uniform, but all the disks lean in one particular direction.

Ten pairs of sensilla auriformia were found on the alloscutum of all larvae of *Rhipicephalus* examined. Five pairs may be seen dorsally some distance from the median line and five pairs on the edge of the alloscutum. Neither capitulum nor scutum seem to have any. Twelve pairs are located on the ventral side, two of them be-

tween the coxæ, the remainder on the opisthosoma, five of the latter in the festoons.

The same number of sensilla auriformia is found in the larvæ of *Hyalomma dromedarii* Koch (Text-fig. 2) as in *Rhipicephalus* and their arrangement is similar. In the larva of *Boophilus calcaratus* Birula (Pl. 3, fig. 7) the pair behind the third coxæ and the first pair on the edge are missing, but the remaining sensilla auriformia are as in the larva of *Rhipicephalus*.

Summary

The larvæ of the Rhipicephalinæ do not possess peculiar integumentary sense organs, as K. W. Neumann (1942) believed, but rather the same types found in the nymphs and adults. The organs are merely in a more primitive state of development and the sensilla laterniformia appear to be missing. Sensilla sagittiformia, sensilla hastiformia and sensilla auriformia may be demonstrated. These organs are strictly specific in number and arrangement within the genera *Rhipicephalus, Hyalomma* and *Boophilus*.

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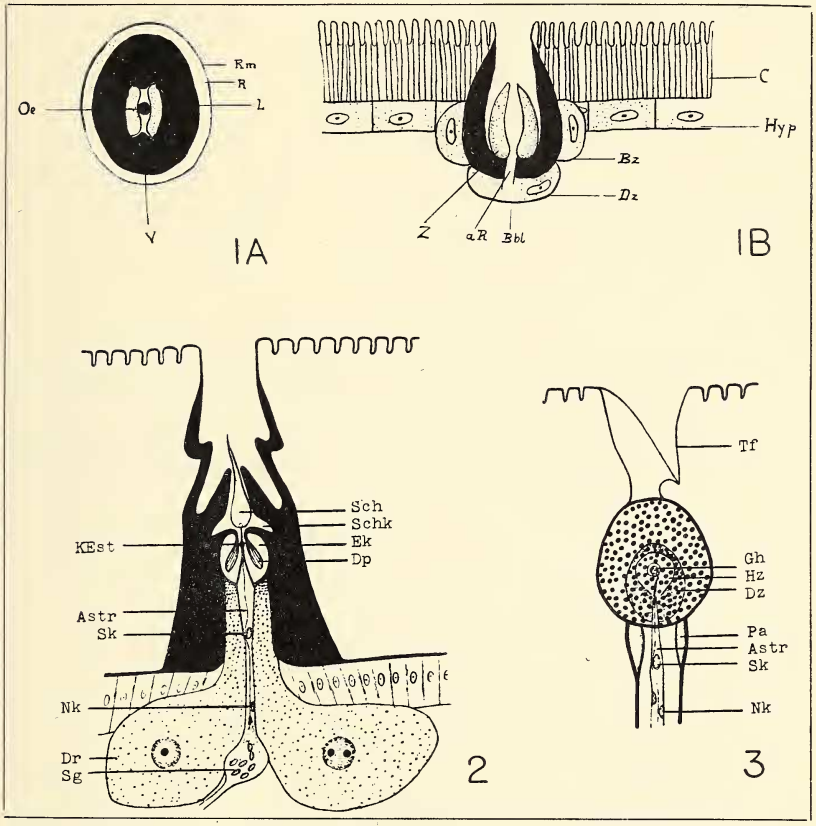
Explanation of Plate 1

Fig. 1. Larval integumentary sense organ of *Haemaphysalis punctata* Can. and Fanz., redrawn from K. W. Neumann (1942). A, in direct view; B, in side view: aR, sensory duct; Bbl, internal vesicle; Bz, generative cell; C, cuticula; Dz, gland cell; Hyp, hypodermis; L, lips; Oe, mouth of the sensory duct; R, frame; Rm, fringe; V, protrusions of the frame; Z, tooth.

Fig. 2. Schematic drawing of a sensillum sagittiforme of *Hyalomma*, after P. Schulze: Astr, axial fiber; Dp, projecting ledges; Dr, gland cell; Ek, terminal chamber; KEst, knot of the scolopale; NK, enveloping cell nucleus; Sch, tuft; Schk, tuft chamber; Sg, sensory cell group outside the duct. The chitinous structure surrounding the sense organ has been omitted.

Fig. 3. Schematic drawing of a sensillum auriforme on the alloscutum of a female *Hyalomma*, after P. Schulze: Astr, axial fiber; Dz, shaded zone of the disk; Gh, papilla with terminal apparatus in central area of the disk; Hz, unshaded zone; Nk, enveloping cell nucleus; Pa, pigmented and thickened section of the duct; Sk, sensory cell nucleus; Tf, supporting plicature. The chitinous structure surrounding the sensory organ and gland cells has been omitted. The disk covering the sensory cell and the terminal apparatus is assumed to be transparent.

PSYCHE, 1949 VOL. 56, PLATE 1



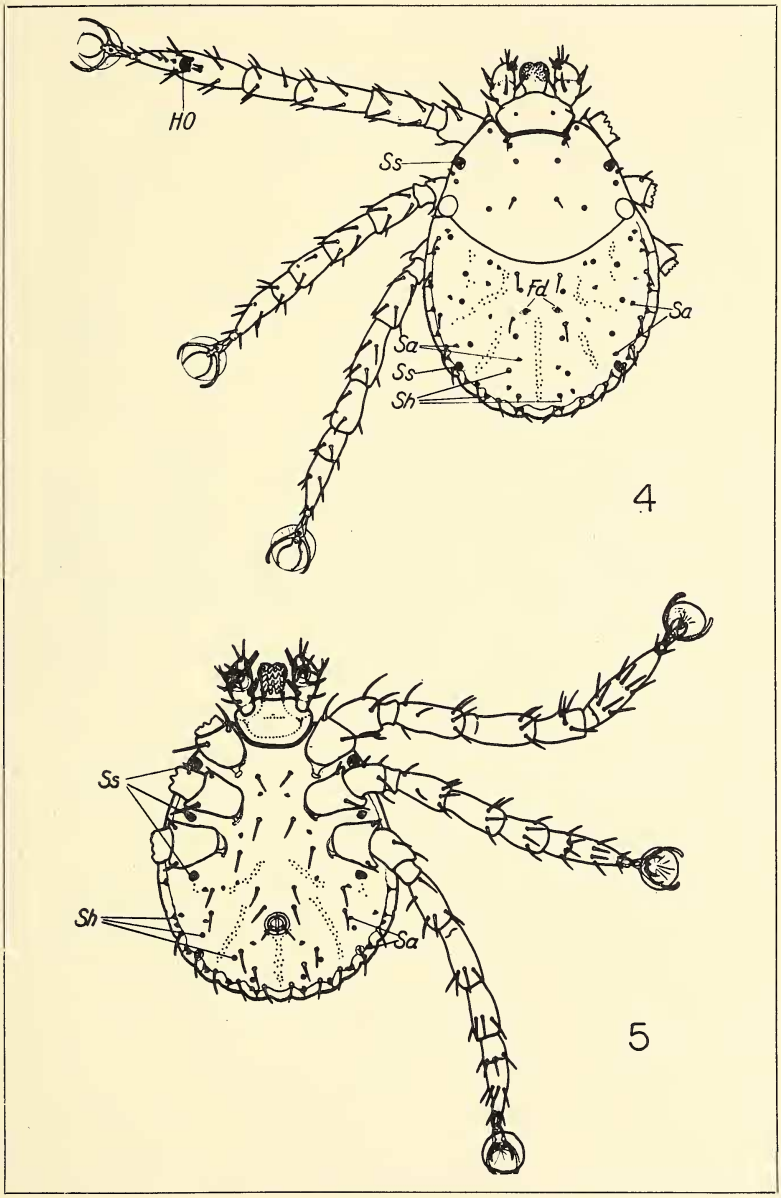
DINNIK AND ZUMPT—RHIPICEPHALINÆ

Explanation of Plate 2

Fig. 4. Dorsal view of larva of *Rhipicephalus appendiculatus* Neum., showing sensory organs: Fd, foveæ dorsales; HO, Haller's organ; Sa, sensilla auriformia; Sh, sensilla hastiformia; Ss, sensilla sagittiformia.

Fig. 5. Ventral view of larva of *Rhipicephalus appendiculatus* Neum., showing sensory organs: Sa, sensilla auriformia: Sh, sensilla hastiformia; Ss, sensilla sagittiformia.

PSYCHE, 1949 VOL. 56, PLATE 2



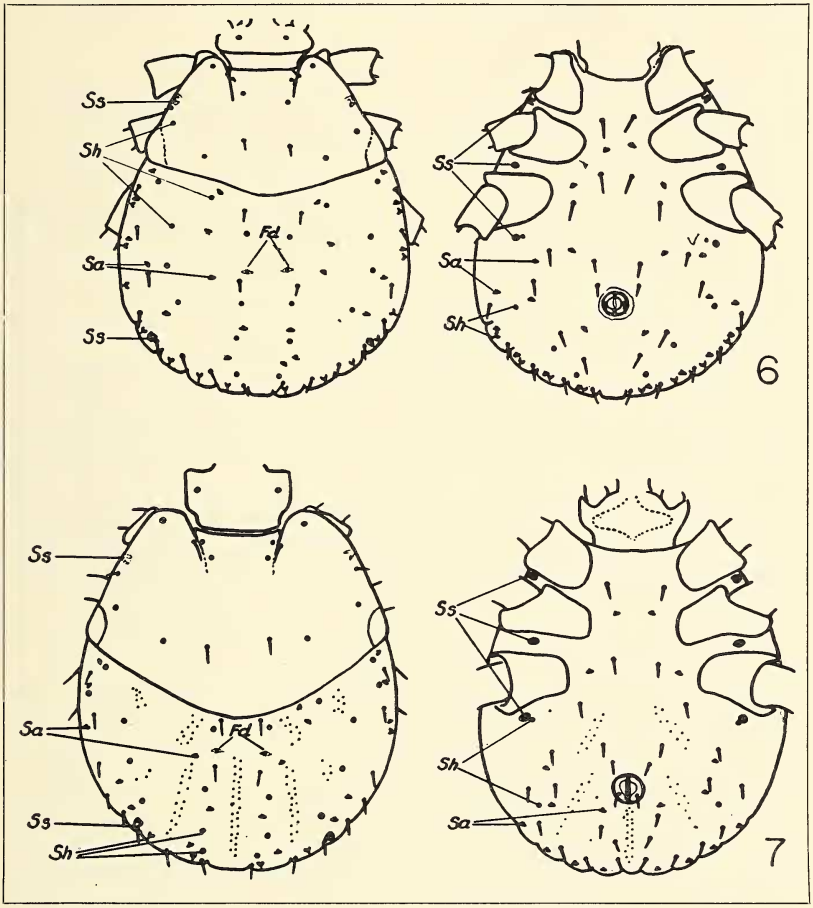
DINNIK AND ZUMPT—RHIPICEPHALINÆ

Explanation of Plate 3

Fig. 6. Arrangement of the integumentary sense organs of the larva of *Rhipicephalus sanguineus* Latr.: Fd, foveæ dorsales; Sa, sensilla auriformia; Sh, sensilla hastiformia; Ss, sensilla sagittiformia.

Fig. 7. Arrangement of the integumentary sense organs of the larva of *Boophilus calcaratus* Birula: Fd, foveæ dorsales; Sa, sensilla auriformia; Sh, sensilla hastiformia; Ss, sensilla sagittiformia.

PSYCHE, 1949 VOL. 56, PLATE 3



DINNIK AND ZUMPT—RHIPICEPHALINÆ